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NOTES ON THE PROTODONATA AND PROTOZYGOPTERA OF THE LOWER PERMIAN OF KANSAS

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A collection of insects from the Permian beds at Elmo, Kansas, made in the summer of 1933 by Alexander B. Klots, V. S. L. Pate, and W. D. Sargent for Ward's Natural Science Establishment of Rochester, New York, included a few Protodonata and Protozygoptera. These, although few in number, were mute but conclusive evidence of the considerable degree of confusion which existed regarding the true nature of several of the species within that group. Through the courtesy and cooperation of Professor E. H. Sellards of the University of Texas, Dr. Carl O. Dunbar of the Peabody Museum at Yale University, and Dr. Reginald Painter of Kansas State College, I was able to make the comparisons that affirmed my suspicions that *Tupus permianus*, *Tupus readi*, *Kennedya mirabilis*, and *Progoneura minuta* had been incorrectly interpreted, and that those errors had been further enhanced by inaccurate drawings. Most of these errors have now been corrected (Carpenter, 1939), and new and helpful material has been described. I should like to add a few notes which I think are of value concerning my material.

The venational terminology employed by Carpenter is followed here. Mistakes may easily be made in translation from one system to another; one author, in his discussion of the genus *Tupus*, refers to his R_{4+5} (the R_3 of Tillyard and M_3 of Comstock-Needham) as R_3 , as R_{3+4} , as R_5 , and as R_{4+5} .

All the material mentioned in this paper except those specimens actually belonging to other people or institutions has been placed in the Department of Insects and Spiders, the American Museum of Natural History.

*Tupus*² *permianus* Sellards

It is to be recalled that when Sellards described this species (1906) he pointed out the presence of oblique veins at the fork of vein R_2 and R_3 (M_1 and M_2) and of a longitudinal intercalary or supplementary vein behind R_3 . He compared these oblique veins with the *subnodal* and *oblique* veins of the Odonata and the intercalary sector with the *bridge* plus the *radial sector*. He considered their presence a substantiation of the Comstock-Needham theory of the crossing over of the radial sector and sufficient cause for making the Protodonata a subordinate group of the order Odonata. Tillyard (1925), upon examination of a photograph of *permianus* sent to him by Sellards, was unable to see any sign of the alleged oblique veins and restored the Protodonata to ordinal rank. Carpenter (1931) redescribed *permianus* from six specimens in the Harvard collection and from sketches and a photograph of the type. His drawing did not show the oblique veins, and we now know that he had no specimens with that portion of the wing preserved.

I think it is rather significant that of the six specimens I have seen of *Tupus* all show one or both of these veins present. Although the type of *permianus* remains lost we can feel confident that Sellards was correct in his description of this detail as he has been proved to be in the others.

I do not consider, as did Sellards, however, that their presence is a substantiation of the Comstock-Needham theory of the

² The genus *Tupus* was established by Sellards (1906, Amer. Jour. Sci., ser. 4, vol. 22, p. 249). In a note in that same journal for 1909, ser. 4, vol. 27, p. 151, in which he changes the name of several genera, he writes "... *Tupus* should read *Typus*." According to Articles 19 and 32 of the International Rules of Zoological Nomenclature (1926, Proc. Biol. Soc. Washington, vol. 39, pp. 35-104), the name should remain in its original form.

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crossing over of the radial sector but rather that it has significant bearing on the refutation of that theory. It is hardly credible that, had the crossing over been accomplished and the proximal bracing by the bridge completed, portions of the strong radial sector would have occasionally dropped out, as seems to be the case in those of my specimens in which the subnodal is present and the oblique is missing (fig. 1); or that the trachea would follow the zigzag course indicated when the subnodal is well distal to the fork (figs. 2, 3). If we consider this material as dating from the period when the Protodonata were all unwittingly experimenting with various devices for support and increased wing efficiency and had yet to stumble upon

base, divergent to the level of the origin of R_s , then convergent towards the apex of the wing. Sc extending out on the wing well beyond the limits of the preserved portion. R_s+M forking from R_1 at a distance of 20 mm. from the base of the wing and one cell beyond the origin of MA. R_{4+5} originating at a distance of 48 mm. from the base of the wing or only about half as far from the base of R_s as from the origin of R_3 which is 101 mm. from the base of the wing. A sector between R_2 and R_3 rises six cells beyond the fork. An intercalary vein rising behind R_{2+3} at a point 86.5 mm. from the base of the wing is at first irregular, then in a few cells straightens out and becomes a strong convex vein paralleling R_{2+3} for a distance of



Fig. 1. Fragment, probably *Tupus*, showing "subnodal" vein at origin of vein R_3 .

or to evolve the nodal region of modern Odonata, how natural it would be to find the weak cross veins variable as to location in relation to the wing axis as well as in their actual presence or absence.

***Tupus readi* Carpenter**

My collection includes two beautifully preserved portions and several small fragments which agree with the corrected description of *readi* (Carpenter, 1939). Since more of the wing area is shown than has hitherto been described, I include them here.

The large specimen (fig. 4) is 124 mm. in length. Precostal space short, extending but little beyond the second cross vein between C and Sc. C and Sc remote at the

about four cells, and then slightly diverges from it to run parallel to R_3 . A strong oblique cross vein between R_1 and R_2 just after the origin of R_3 is in line with another oblique vein between R_3 and the intercalary vein. R_{4+5} is unbranched. Two cell rows between the intercalary vein and R_{4+5} at the level of the origin of R_3 , the lower row slightly wider than the upper. MA and R_s at first divergent and then convergent toward the origin of R_{4+5} ; MA then continues parallel to R_{4+5} . The first branch of MA rises 20 mm. or about 11 cells beyond the origin of R_{4+5} . Obsolescent base of Cu_1 present. Cu_2 unbranched, strongly undulate. Two oblique veins present between Cu_2 and A in the region of the anal crossing, slightly

more than halfway from the base of the wing to the origin of 2d A; each of these oblique veins is considerably stronger than a normal cross vein. First A less strongly sigmoid than Cu_2 , pectinately branched apically. Second A originating at the level of the origin of R_s+M . Anal angle of the wing angulate and characterized by the presence of greatly elongated

tion, measuring 111 mm., is larger. The "subnodal" vein is present and is two and a half cells before the origin of R_3 , but the "oblique" is not present. The space between the origin of R_3 and the vein R_{4+5} is greater than in the other material due to the unusual height of the cell row just above R_{4+5} . The first branch of MA rises nearer the level of the origin of R_{4+5} , the

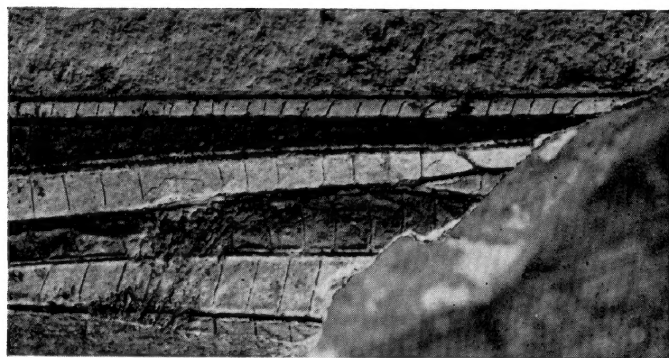


Fig. 2. Fragment, probably *Tupus*, showing "subnodal" vein beyond origin of vein R_3 .

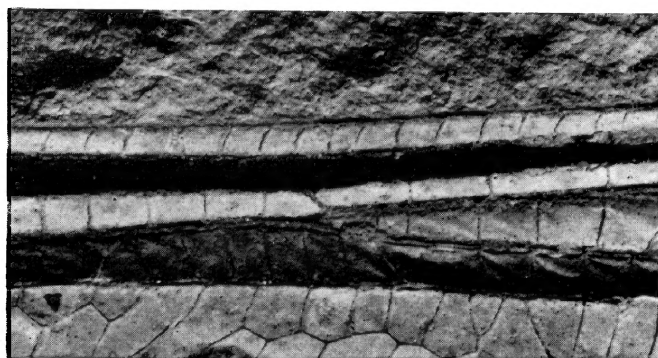


Fig. 3. *Tupus readi* Carpenter. Enlargement of portion of figure 4 showing "subnodal" and "oblique" veins beyond the origin of R_3 .

cells extending from the anal vein to the wing margin for a distance of 10 cells.

My specimens differ from Carpenter's corrected figure of *readi* only in the presence of the oblique veins at the origin of R_3 (fig. 4), in the slightly more proximal position of R_{4+5} , and in the presence of the oblique veins in the region of the anal crossing.

Another specimen (fig. 5) in this collec-

tion, measuring 11 mm., or eight cells apart. The relation of 2d A with the parallel veins on either side is more like *Tupus* at the level of the fork of R_{4+5} than it is like *Megatypus*. But now that we know of the error in the definition of *Megatypus* in regard to the supposed distal origin of R_{4+5} , it is difficult to distinguish between these two genera when only this area of the wing is available.

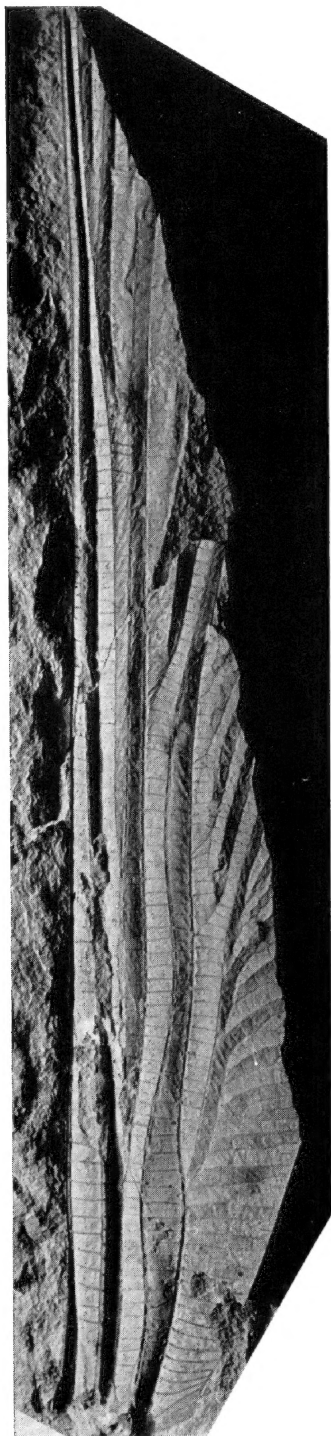


Fig. 4. *Tupus readi* Carpenter.



Fig. 5. *Tupus readi* Carpenter.

In the collection of the Kansas State College at Manhattan, Kansas, there is a fine wing collected by J. W. McCulloch which is also of this species. It is slightly smaller than the type. The first branch of MA rises 10 mm. or seven cells beyond the origin of R_{4+5} .

These three specimens differ from the type in size, but the difference is not inconsistent with individual variation. That portion of the wing extending from the apex of the second arch of Cu_2 to the origin of R_3 (taken because it is the only portion comparable in the four specimens) measures, respectively, 52, 66, and 43 mm.

lowers the curve of the wing tip and arches strongly downward. Sc fuses with the costa before the origin of R_{4+5} . Vein R_1 approaches the costa rather abruptly about one-third of the way between the origin of R_{4+5} and the apex of the wing, and from that point vein C seems to form a thickened cord-like border to the wing. This thickening may be due to a folding under of the wing margin, but its ridge-like quality makes that seem unlikely. An oblique cross vein lies between veins R_1 and R_{2+3} at a point about halfway between the approximation of R_1 and C and the apex of the wing. The recurrence of

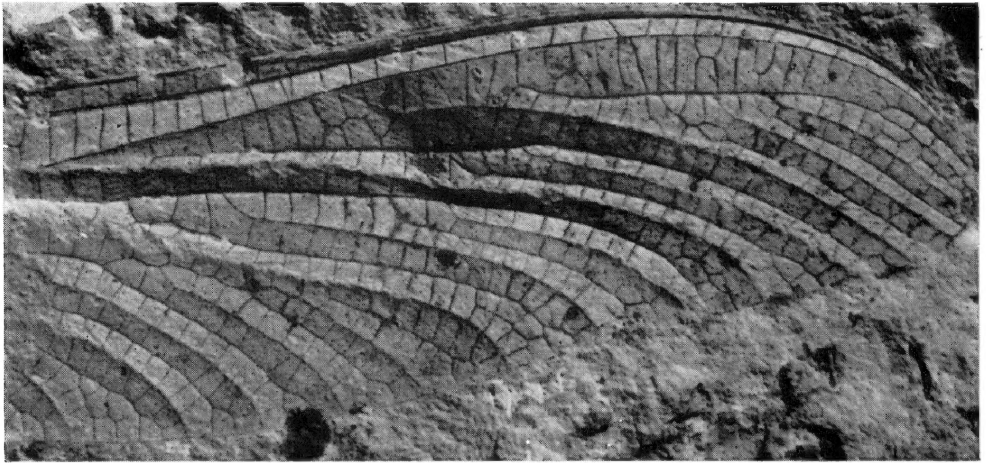


Fig. 6. *Oligotypus tillyardi* Carpenter.

The specimens that I have seen of *T. readi* do not show the hooking of the vein tips which is so conspicuous in the photograph of the type of *permanus* sent to me by Sellards. The drawing of *M. vetustus* (Carpenter, 1933, p. 416), later identified as *permanus* (Carpenter, 1939), does not show it either, but this may be the artist's error.

***Oligotypus tillyardi* Carpenter**

One of my specimens, measuring 24 mm. from the origin of R_{4+5} to the apex of the wing, is probably of this species (fig. 6). The apex is considerably more rounded than that shown in the figure of the type (Carpenter, 1931, p. 107). Vein R_2 fol-

lows the curve of the wing tip and arches strongly downward. Sc fuses with the costa before the origin of R_{4+5} . Vein R_1 approaches the costa rather abruptly about one-third of the way between the origin of R_{4+5} and the apex of the wing, and from that point vein C seems to form a thickened cord-like border to the wing. This thickening may be due to a folding under of the wing margin, but its ridge-like quality makes that seem unlikely. An oblique cross vein lies between veins R_1 and R_{2+3} at a point about halfway between the approximation of R_1 and C and the apex of the wing. The recurrence of

***Kennedya mirabilis* Tillyard**

The drawing that accompanies the original description of the type of this species (Tillyard, 1925, p. 64, fig. 10) differs slightly from the photograph of the same specimen published in the same article (p. 67, fig. 12A). A second and composite drawing published later (Tillyard, 1928, p. 163, fig. 6) shows still greater dissimilarity

to the photograph. A copy of this second drawing (Carpenter, 1931, p. 117, fig. 4) has further increased the discrepancies and has created a misunderstanding regarding the true nature of the genus. A more recent drawing (Carpenter, 1939, p. 46) is more accurate.

I have examined the type of *Kennedya mirabilis*, Specimen No. 5006 a-b, in the Yale University collection and wish to emphasize the following facts regarding it. Veins Sc and C converge at equal obliquities to form the nodus, as described by Tillyard, but do not make a distinct break in the costa as his and subsequent drawings indicate. Vein R_1 curves slightly upward at its origin, although viewed from

mm. in the type is but 18 mm. long in this specimen. It agrees with the type except that the costa is more nearly straight and that vein R_s is slightly less arched at its origin.

Kennedya (*Progoneura*) *minuta*
Carpenter

Kennedya mirabilis and *Progoneura minuta* are distinguished by characters of degree and not of difference, and I believe that they can no longer be considered as of separate genera. The costa of *minuta* is straight at the nodus, the costa of the type of *mirabilis* is less broken than the author of *minuta* believed it to be, and in the specimen of *mirabilis* in my collection it is even

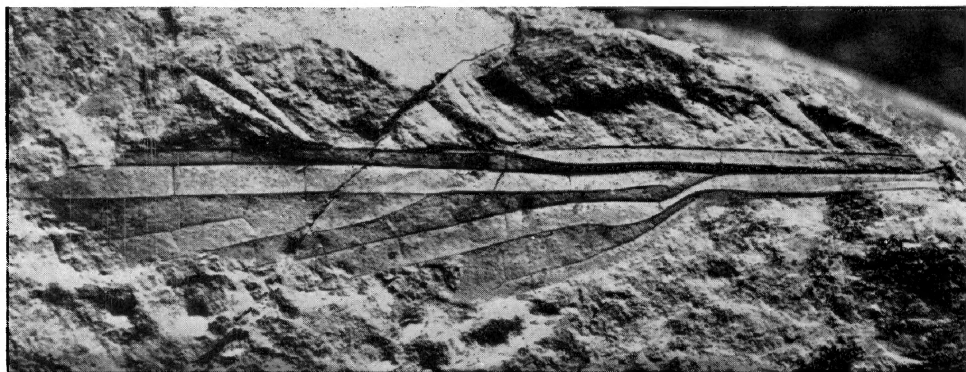


Fig. 7. *Kennedya*.

some angles this upward bend is imperceptible. R_s originates more than halfway down on the arculus and arches upward at its origin rather more abruptly than figured hitherto. MA is deflected at the point of the cross vein m-cu and does not follow the curve of the arculus. Cu_2 does not follow a straight course through the petiole but is slightly undulate. First A rises at the apex of the undulation of Cu_2 and diverges from it gradually, forming a long, triangular subquadrangle with anterior and posterior sides curved as described by Tillyard.

A specimen in my collection having the preserved portion of the wing measuring 29 mm. (fig. 7) is somewhat smaller than the type, for a portion measuring 25.6

more like that of *minuta*. Vein R_1 in *minuta* is almost straight at its origin; in *mirabilis* it curves but slightly and at some angles appears to be straight. Vein R_s in the type of *minuta* is nearly straight at its origin and rises at the middle of the arculus. This I had thought to be a true difference between the two species, but Carpenter has a new specimen of *minuta* (1939) which shows the location and manner of origin of R_s to be nearly identical with that of *mirabilis*. The deflection of MA, the undulation of Cu_2 within the petiole, and the shape of the subquadrangle are seen now to be similar also.

There is in my collection a specimen (fig. 8) which I had determined as *minuta* because of its small size. The preserved

portion of the wing measures 16 mm., while the corresponding portion of the larger wing described above as *mirabilis* measures 26 mm. But Carpenter (1939) has now shown that size is not a criterion. This leaves only the length of 1st A as a point of difference between them. In *mirabilis*, 1st A surmounts five and one-half cells (Carpenter, 1939) beyond the quadrangle, and in *minuta* it surmounts only one cell. This seems like a significant difference,

until we find that *K. tillyardi* has been described (Carpenter, 1939) as having 1st A surmounting three and one-half cells, that my larger specimen (fig. 7) has it surmounting two and one-half cells, and that my smaller one (fig. 8) has it surmounting one and one-half cells. It remains, then, to determine whether *mirabilis* and *minuta* are the same or whether each of the known specimens should be described as a separate species.

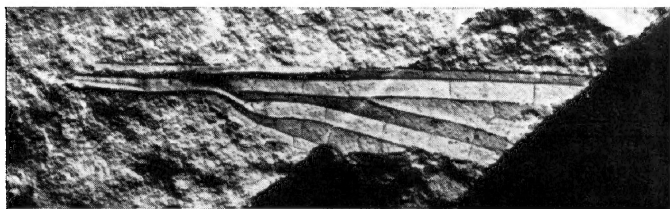


Fig. 8. *Kennedyya*.

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